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Molluscan Community Recovery Following Partial Tidal Restoration of a New England Estuary, U.S.A.

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Abstract

Historic human-imposed tidal flow restrictions at many New England estuaries have resulted in dramatic alteration of estuarine community structure and function. East Harbor, a 291-ha coastal lagoon and salt marsh in Truro, Massachusetts, was artificially isolated from Cape Cod Bay in 1868. After the isolation, salinity decreased to near freshwater levels, and estuarine fish and invertebrate populations declined precipitously. Partial tidal flow was restored to East Harbor in 2002; since then, East Harbor has experienced substantial increases in salinity, and native fauna has begun to return to the system. The objective of this study was to obtain information on marine molluscan populations recolonizing East Harbor. Using a combination of benthic cores and direct searching, we surveyed 50 plots throughout the estuary in July and August 2005. We detected 16 molluscan species in East Harbor as a whole; the four most abundant species were *Mya arenaria*, *Littorina* spp., *Mytilus edulis*, and *Mercenaria mercenaria*. We found significant differences in species richness and abundance of these species among three regions of East Harbor that varied markedly in salinity and distance to Cape Cod Bay; diversity and abundance were both highest in Moon Pond, which has a direct connection with sources of seawater and marine biota, and lowest in the northwest cove, which receives high freshwater discharge. These findings demonstrate the effectiveness of Cape Cod National Seashore's preliminary tidal restoration efforts while underscoring the continued need for full tidal restoration at East Harbor and other tide-restricted estuaries.

Key words: benthic, estuary, mollusc, *Mya arenaria*, New England, tidal restoration.

Introduction

The practice of diking, draining, and impounding estuarine ecosystems for agriculture, flood protection, mosquito control, waterfowl habitat, and construction of roads and railways has an extensive history in Europe and the western North Atlantic. In New England, at least half of the salt marshes present at the time of European settlement were diked and/or filled by the mid-1970s (Nickerson 1978; Rozsa 1995).

Tidal restrictions from diking and impounding profoundly alter the ecological structure and function of estuarine ecosystems. Loss of tidal energy and subsequent reductions in water and soil salinity lead to altered sediment chemistry and biogeochemical cycling (Portnoy & Giblin 1997), seasonal dissolved oxygen depletion (Portnoy 1991), marsh subsidence (Roman et al. 1984, 1995; Burdick et al. 1997), replacement of native salt marsh grasses (e.g., *Spartina* spp.) with near monocultures of the invasive reed *Phragmites australis* (Roman et al. 1984; Sinicrope et al. 1990), reduced faunal diversity and abundance (Herke et al. 1992; Burdick et al. 1997; Raposa 2002; Warren et al. 2002; Raposa & Roman 2003), and reduced biological exchange with adjacent coastal waters (Roman et al. 1984; Herke et al. 1992). Tidal restrictions also prevent the landward migration of coastal marshes, thereby limiting the ability of coastal systems to respond to sea level rise associated with global climate change (Pethick 1993).

Throughout New England, efforts are underway to reestablish natural hydrologic regimes at tide-restricted estuaries by removing dikes and tide gates, installing culverts, and replacing small culverts and bridges with larger openings (Sinicrope et al. 1990; Roman et al. 1995; Fell et al. 2000; Warren et al. 2002; Konisky et al. 2006). The timescale for recovery of specific estuarine functions within these restored systems varies from days to decades. Increased pore water salinity, reduced abundance of salt-intolerant vegetation, and nekton community recovery can occur rapidly after tidal restoration (Burdick et al. 1997; Raposa 2002; Roman et al. 2002; Warren et al. 2002; Konisky et al. 2006), whereas marsh elevation and bird, macroinvertebrate, and salt marsh plant communities may require well over 20 years for full recovery (Burdick et al. 1997; Fell et al. 2000; Warren et al. 2002).

Estuarine restoration monitoring has primarily focused on hydrology, vegetation, nekton, and birds (Neckles et al. 2002), and existing research on macroinvertebrate populations in restored estuaries has been largely limited to nekton and marsh-dwelling species (Peck et al. 1994; Fell et al. 2000; Raposa 2002; Roman et al. 2002). However,

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benthic macroinvertebrates play a key role in sediment–water column nutrient cycling and are an important food source for fish, birds, mammals, and other macroinvertebrates (Dauer 1993). In addition, they have been identified as strong indicators of estuarine health because they are relatively sedentary and therefore cannot avoid deteriorating water or sediment quality (Dauer 1993). Further, in regions like New England, where bivalve molluscs are culturally and commercially valuable (Belding 1909, 1930; MacKenzie et al. 2002*a*, 2002*b*), the reestablishment of diverse, abundant benthic molluscan communities is of special interest.

Cape Cod National Seashore manages 1,010 ha of diked coastal wetlands, including substantial portions of the four largest diked estuaries on Cape Cod (Portnoy et al. 2003). Tidal restoration efforts are in progress at all four sites. The goal of this study was to provide information on molluscan community recovery at East Harbor, one recently restored site, for use in the Seashore's long-term estuarine monitoring and management programs. Our specific objective was to document species richness, abundance, and distribution of benthic molluscan communities recolonizing East Harbor 3 years after partial tidal flow was restored to the system.

Methods

Study Site

East Harbor (lat 42°03′33″N, long 70°07′43″W), Massachusetts, U.S.A., is a 291-ha coastal lagoon and salt marsh that originally functioned as an estuary, connected to Cape Cod Bay by an inlet at its western end (Fig. 1). In 1868, it was completely isolated from Cape Cod Bay by the construction of a solid-fill causeway for trains and automobiles (Portnoy et al. 2005). After the construction of the dike, salinity throughout East Harbor decreased to near freshwater conditions, sand from migrating dunes to the northwest shoaled the impounded "lake" to an average depth of 1.3 m, and the waters became highly eutrophic with large blooms of nitrogen-fixing cyanobacteria (Applebaum & Brenninkmeyer 1988). The tidal restriction also led to chronic summertime oxygen stress, with subsequent decreases in fish and invertebrate diversity and abundance. In September 2001, approximately 40,000 juvenile Alewife (*Alosa pseudoharengus*) and several hundred White perch (*Morone americana*) perished in East Harbor, likely due to extreme oxygen depletion resulting from the lack of tidal exchange. In December 2001, this massive fish kill prompted an experimental opening of the approximately 2-m-diameter drainage pipe that connects the south end of the system to Cape Cod Bay (Portnoy et al. 2005).

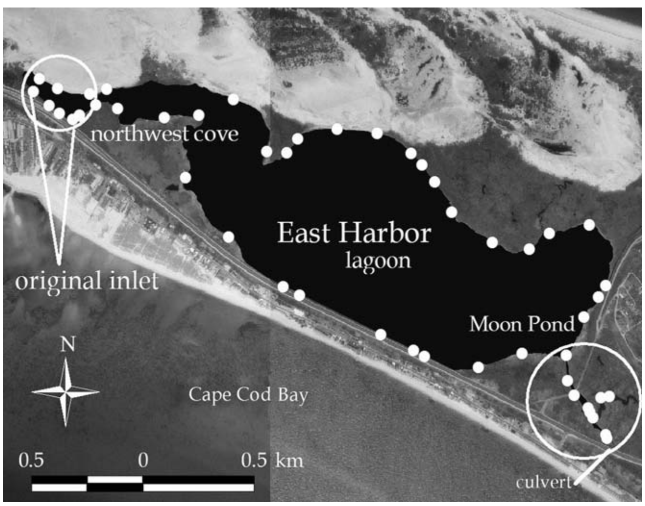

Figure 1. Molluscan sampling points at East Harbor, Truro, Massachusetts. Sampling was spatially stratified within three areas of East Harbor that varied in salinity and distance to Cape Cod Bay: Moon Pond, the lagoon, and the northwest cove. (Orthophoto from MassGIS.)

The culvert connecting East Harbor to Cape Cod Bay was permanently opened in November 2002. Since then, salinity in the main lagoon has increased to approximately 25 ppt, and Moon Pond creek, which receives seawater directly from the culvert, routinely reaches salinity levels of 30 ppt. Salinity in the northwest cove, which receives high freshwater discharge from the Pilgrim groundwater lens, still only ranges from 15 to 20 ppt (Portnoy et al. 2005). The tidal range in Moon Pond has increased minimally (<0.5 m compared to 2.5–3.5 m at a nearby unrestricted site), but the flood tide volume remains too low to create significant tidal fluctuations in the lagoon or northwest cove (Portnoy et al. 2006).

Extensive beds of submerged aquatic vegetation, primarily Widgeongrass (*Ruppia maritima*) and Eelgrass (*Zostera marina*), reappeared throughout the lagoon and northwest cove as early as 2003 (Portnoy et al. 2005). By September 2004, at least 15 species of estuarine fish, crustaceans, and invertebrates, including Northern quahog (*Mercenaria mercenaria*), Softshell clam (*Mya arenaria*), and Blue mussel (*Mytilus edulis*), had also reestablished populations in East Harbor (Portnoy et al. 2005).

Sampling Methods

Molluscan species richness and abundance (measured as individuals/m^2) were surveyed from 10 July to 26 August 2005. Sampling was spatially stratified within three areas of East Harbor that varied markedly in salinity and distance to Cape Cod Bay: Moon Pond, the central lagoon, and the northwest cove (Figs. 1–3). One hundred forty random sampling points were initially generated in ArcView GIS 3.2 (Environmental Systems Research Institute, Inc. 1999); 50 of these points were systematically selected to ensure that sampling was evenly distributed throughout each region. To account for the central lagoon's proportionately larger area, we selected 30 points in the lagoon,

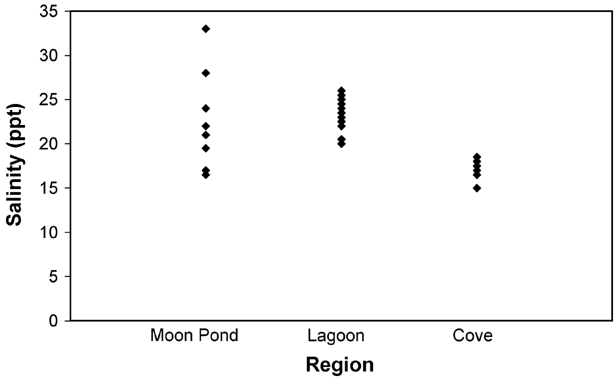

Figure 2. Salinity at East Harbor, Truro, Massachusetts, by region.

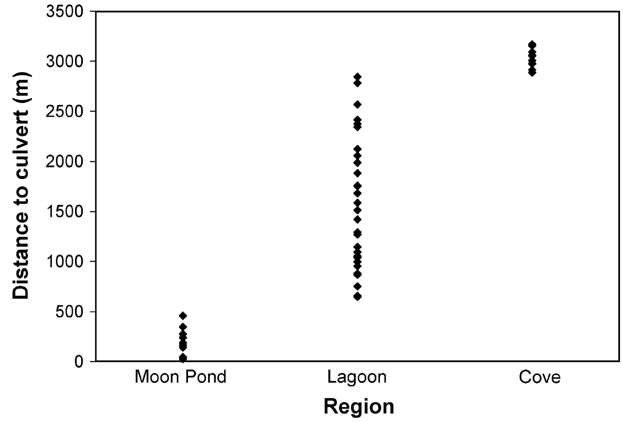

Figure 3. Distance to the culvert connecting East Harbor to Cape Cod Bay, Truro, Massachusetts, by region.

10 points in Moon Pond, and 10 points in the northwest cove. Digging and sieving were not possible at water depths greater than 1 m, so all sampling points were located along the shoreline, where water was less than 1 m deep. To reduce variation in species richness, density, and size class data due to water depth, molluscs were consistently sampled at a water depth of approximately 0.3 m. To reduce biases in size class data associated with seasonal growth, sampling times and locations were rotated so that each region was sampled evenly throughout the field season. All points were sampled twice, no more than 1 week apart.

At each point, gastropod and bivalve molluscs were sampled using a combination of benthic cores and digging within a 0.45-m^2 quadrat (Dethier & Schoch 2005). Sediment in each quadrat was excavated to a depth of approximately 20 cm (Dauer et al. 1987) using a shovel and then wet-sieved through 0.64-cm mesh to detect species that grow to lengths greater than 0.6 cm (hereafter "shovel method"). After shoveling, each quadrat was manually searched for any remaining molluscs. To ensure thorough sampling, after hand searching, we continued shoveling sediment out of each quadrat until five consecutive shovelfuls were devoid of molluscs. One 10-cm-diameter benthic core was also collected immediately adjacent to each quadrat. Sediment from each core was wet-sieved through 2-mm mesh to detect juvenile molluscs and species such as Amethyst gemclam (*Gemma gemma*) that do not exceed 0.6 cm in length (hereafter "benthic core method"; Dethier & Schoch 2005).

All molluscs retained on the sieves were counted live, identified to genus or species, and classified into one of three size classes: less than 2 cm, 2–4 cm, or greater than 4 cm. *Mercenaria mercenaria* and *Mya arenaria* that met legal size limits for commercial and recreational harvesting (2.54 cm hinge width and 5.08 cm anterior–posterior length, respectively) were also recorded as "harvestable." Molluscan identification was according to Weiss (1995). Salinity was measured at each sampling point using a handheld refractometer (Sper Scientific Model 300011; Scottsdale, AZ, U.S.A.).

Data Analysis

Molluscan species richness, density, and size class data were compared among the three regions of East Harbor. Species richness for each sampling point was defined as the total number of species detected across both sampling methods and events; density and size class data for each point were calculated as the mean of both sampling events. Only four species occurred with enough regularity to warrant detailed investigations into their density and size class distribution: *Mya arenaria*, *Me. mercenaria*, *Myt. edulis*, and Periwinkle (*Littorina* spp.). Thus, only data for these four species were analyzed statistically.

The shovel method did not detect animals smaller than 0.64 cm and thus did not represent the density of molluscs in the smallest size class as fully as the benthic core method, which could detect animals as small as 2 mm. Similarly, because each benthic core only sampled an area of 78.5 cm^2, the benthic core method did not accurately represent the density of larger molluscs, which must be sampled across a larger area. Therefore, with the exception of *Littorina* spp., all density data for the larger size classes (2–4 cm, >4 cm, and harvestable) derive from the shovel method, and all density data for the smallest size class (<2 cm) derive from the benthic core method. *Littorina* greater than 2 cm in length were not found at East Harbor; as a result, these species were always classified into the smallest size class (<2 cm). However, the shovel method was much more efficient at detecting *Littorina*; thus, analysis of *Littorina* species density only includes data collected with the shovel method. For all other species, we excluded animals of the smallest size class (<2 cm) that were detected with the shovel method, as well as larger animals ($\geq$2 cm) that were detected with the benthic core method. Additionally, because *Littorina* are highly mobile, it is likely that some *Littorina* individuals escaped detection, particularly in densely populated quadrats that took a long time to sample; data for this species thus represent minimum densities.

Species richness and density data were nonnormally distributed due to the naturally patchy distribution of molluscan communities, and data transformation did not improve normality. Therefore, nonparametric tests were used to assess differences in species richness, density, size class distribution, and molluscan community composition among the three regions of East Harbor. Separate Kruskal–Wallis tests (Zar 1999) were used to compare species richness and density of each of the four most abundant species and the densities of different size classes for the three most abundant species, excluding *Littorina*, among the three regions of East Harbor. Species richness for each region was also estimated using the jackknife procedure (Heltshe & Forrester 1983); this technique provides a more robust estimate of species richness than raw species counts for naturally patchy biological communities because it accounts for both the sample size and the number of infrequently detected species.

Molluscan species assemblages among the three regions of East Harbor were compared with a one-way analysis of similarity (ANOSIM) using a Bray–Curtis similarity index (Clarke & Warwick 2001). Three pairwise comparisons (Moon Pond vs. lagoon, Moon Pond vs. northwest cove, and lagoon vs. northwest cove) were also conducted with ANOSIM, and similarity percentages (SIMPER) were calculated to determine which species were most responsible for differences in community composition (Clarke & Warwick 2001). To retain quantitative information for all species while downplaying the influence of dominants in both the ANOSIM and the SIMPER analyses, species assemblage data were square root transformed.

Distance between the culvert and each sampling point was estimated in ArcView GIS 3.2 (Environmental Systems Research Institute, Inc. 1999). Separate Spearman rank correlations (r_s) were used to detect relationships between salinity, distance to culvert, and species richness and salinity, distance to culvert, and density of the four most abundant species (Zar 1999). Statistical significance for all tests was determined at $p \leq 0.05$.

Results

Species Richness

Sixteen molluscan species were detected at East Harbor: 13 occurred in Moon Pond, nine occurred in the central lagoon, and two occurred in the northwest cove; jackknife estimates of species richness were slightly higher (Figs. 4 & 5). An additional species, Eastern oyster (*Crassostrea virginica*), was not present in our sample plots but was observed in both Moon Pond and the lagoon. Molluscan species richness was significantly different among the three regions of East Harbor (Kruskal–Wallis $\chi^2 = 24.81$, $p < 0.0001$; Fig. 5); species richness was highest in Moon Pond and lowest in the northwest cove. Species richness throughout East Harbor was positively correlated with salinity ($r_s = 0.542$, $p < 0.0001$) and negatively correlated with distance from the culvert connecting East Harbor to Cape Cod Bay ($r_s = -0.731$, $p < 0.0001$).

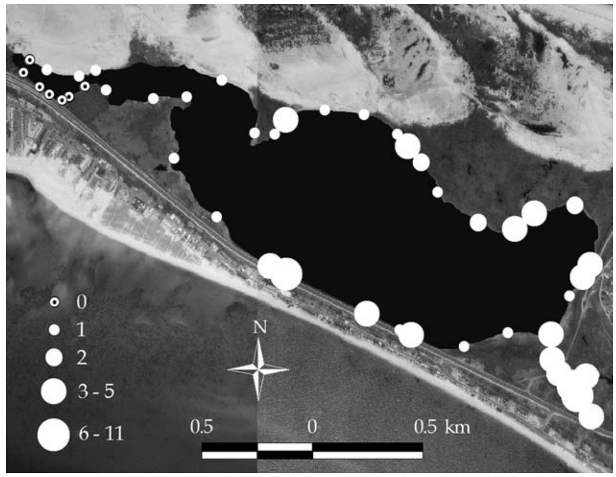

Figure 4. Molluscan species richness distribution at East Harbor, Truro, Massachusetts. Circles represent the total number of species detected at each sampling point. (Orthophoto from MassGIS.)

Abundance

Mean densities of *Mercenaria mercenaria*, *Mya arenaria*, *Mytilus edulis*, and *Littorina* spp. were significantly different among the three regions of East Harbor; for all four species, density was highest in Moon Pond and lowest in the northwest cove (Table 1; Fig. 6). Density of all four species was negatively correlated with distance from the culvert connecting East Harbor to Cape Cod Bay; *Mya arenaria* and *Littorina* spp. density were also positively correlated with salinity (Table 2).

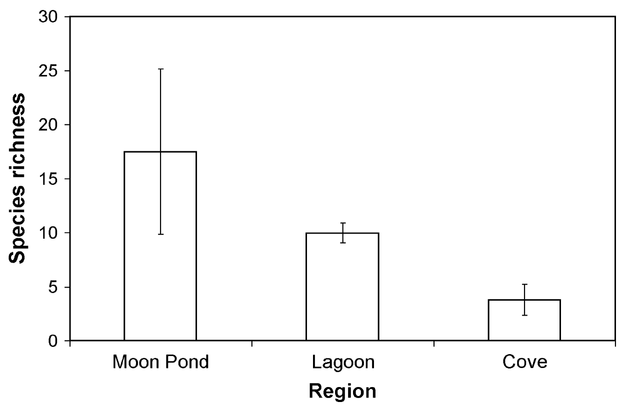

Figure 5. Mean species richness (± SE) at East Harbor, Truro, Massachusetts, by region, as estimated with the jackknife procedure (Heltshe & Forrester 1983). Jackknife calculations are slightly higher than raw species counts (Table 1; Fig. 4) because jackknife estimates account for additional species that may have been missed in sampling efforts due to the naturally patchy distribution of macrobenthic communities.

Table 1. Mean density ± SE and results of Kruskal–Wallis tests for differences in the mean densities of mollusc species at East Harbor, Truro, Massachusetts, by region.

Species	*Moon Pond (individuals/m²) n = 10*	*Lagoon (individuals/m²) n = 30*	*Cove (individuals/m²) n = 10*	χ^2	*p*
Mya arenaria	3,178.33 ± 1,809.94	2,971.09 ± 726.64	0.22 ± 0.22	20.92	<0.0001
Mytilus edulis	47.25 ± 32.94	0.04 ± 0.04	0	17.44	0.0002
Littorina spp.	42.46 ± 30.25	0.96 ± 0.39	0	10.23	0.0060
Mercenaria mercenaria	18.06 ± 13.57	4.43 ± 3.05	0	10.86	0.0044
Gemma gemma	178.25 ± 118.46	0	0	—	—
Mulinia lateralis	0	6.37 ± 4.68	0	—	—
Anomia spp.	3.22 ± 3.22	0	0	—	—
Euspira heros	1.11 ± 1.11	0	0	—	—
Ensis directus	1.00 ± 0.71	0	0	—	—
Geukensia demissa	0	0.81 ± 0.39	0.11 ± 0.11	—	—
Nucella lapillus	0.22 ± 0.22	0	0	—	—
Macoma balthica	0.11 ± 0.11	0	0	—	—
Tagelus plebeius	0.11 ± 0.11	0	0	—	—
Order Cephalaspidea	*	*	*	—	—
Petricola pholadiformis	*	*	*	—	—
Spisula solidissima	*	*	*	—	—
Total	3,470.46 ± 1,810.01	2,983.70 ± 725.66	0.33 ± 0.23	—	—

With the exception of *Littorina* spp., this analysis excludes animals of the smallest size class (<2 cm) that were detected with the shovel method, as well as larger animals (≥2 cm) that were detected with the benthic core method. Asterisks indicate species for which low numbers of small (<2 cm) individuals were detected with the shovel method only; thus, although these species are represented in species richness analyses, they are not included in density calculations. Dashes indicate species that occurred too infrequently to allow for statistical analyses of their densities.

Size Class

We found no harvestable *Me. mercenaria* in East Harbor and no significant difference in the abundance of harvestable *Mya arenaria* among the three regions of East Harbor (Table 3). We did, however, detect a significant difference in the density of mid-size (2–4 cm) *Me. mercenaria* and all three size classes (<2, 2–4, and >4 cm) of *Mya arenaria* and *Myt. edulis* among the three regions of East Harbor (Table 3). Densities across all three species and size classes were highest in Moon Pond and lowest in the northwest cove (Table 3).

Community Composition

Species assemblages were significantly different among the three regions of East Harbor (ANOSIM $R = 0.637$,

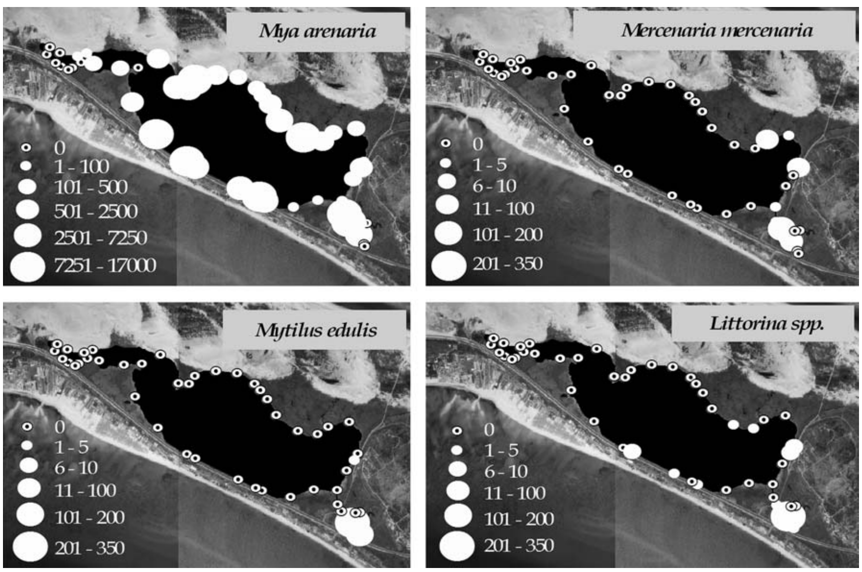

Figure 6. Distribution of *Mya arenaria*, *Mercenaria mercenaria*, *Mytilus edulis*, and *Littorina* spp. at East Harbor, Truro, Massachusetts. Circles represent the density (individuals/m^2) of each species at each sampling point. (Orthophoto from MassGIS.)

Table 2. Spearman rank correlation coefficients (r_s) between species density, salinity, and distance to culvert for the four most abundant mollusc species at East Harbor, Truro, Massachusetts.

Species	*Salinity r_s*	*p*	*Distance r_s*	*p*
Mercenaria mercenaria	0.16	0.2611	**−0.45**	**0.0011**
Mya arenaria	**0.81**	**<0.0001**	**−0.30**	**0.0332**
Mytilus edulis	0.05	0.7211	**−0.54**	**<0.0001**
Littorina spp.	**0.28**	**0.0478**	**−0.56**	**<0.0001**

Bold type indicates statistical significance at $p \leq 0.05$.

$p < 0.0001$). There were significant differences in species assemblages between Moon Pond and the lagoon (ANOSIM $R = 0.402$, $p < 0.0001$) and between Moon Pond and the northwest cove (ANOSIM $R = 0.473$, $p < 0.0001$); however, the most highly significant difference occurred between the lagoon and the northwest cove (ANOSIM $R = 0.865$, $p < 0.0001$).

Mya arenaria contributed over 35% to the aggregate dissimilarity of assemblages for all three pairwise comparisons (Moon Pond vs. lagoon, Moon Pond vs. northwest cove, and lagoon vs. northwest cove; Table 4). *Gemma gemma* also contributed to the dissimilarity between Moon Pond and the lagoon (10.8%), and *G. gemma*, *Myt. edulis*, and *Littorina* spp. contributed to the dissimilarity between Moon Pond and the northwest cove (18.0, 13.4, and 10.9%, respectively; Table 4).

Discussion

Molluscan species richness and abundance at East Harbor were highest in Moon Pond, which has a direct connection with marine sources of seawater and biota, and decreased with increasing distance from the culvert connecting East Harbor to Cape Cod Bay. Accordingly, species richness and abundance of *Mercenaria mercenaria*, *Littorina* spp., and *Mytilus edulis* were more strongly correlated with distance to inlet than with salinity. However, research in other North American estuaries has identified salinity as the most significant factor affecting macrobenthic community structure, with both species richness and abundance increasing with increasing salinity (Dauer 1993; Hyland et al. 2004; Kennish et al. 2004; Dethier & Schoch 2005). At this early stage in the restoration process, distance to the biotic communities of Cape Cod Bay may strongly influence molluscan species richness and abundance at East Harbor because organisms are still migrating from the Bay into the newly reestablished estuary. As molluscs continue to colonize the site, however, salinity will likely replace distance to inlet as the primary factor affecting species richness and abundance throughout the system. This shift is already occurring in populations of *Mya arenaria*, which is the most widely distributed mollusc species at East Harbor and also the only species for which the correlation between salinity and density was highly significant.

The scale and rate of community recovery in restored estuarine ecosystems largely depend on the degree of saltwater exchange. Estuarine structure and function return relatively quickly when tidal flow is unrestricted, although sites with only partial tidal exchange may never fully recover without additional modification of the hydrologic regime (Burdick et al. 1997). Our results demonstrate that, like nekton communities, molluscan communities begin to recover almost immediately after tidal exchange has been restored. However, increased tidal flushing is still needed for full restoration of benthic macroinvertebrate populations. Although molluscan salinity requirements vary greatly according to species, geographic range, and even life stage (Stanley & DeWitt 1983; Newell & Hidu 1986; Newell 1989), salinity in the northwest cove of East Harbor likely remains too low to support complex molluscan communities (Dauer 1993; Bourget et al. 2003). Further, the infusion of aerated seawater through the culvert

Table 3. Mean density ± SE and results of Kruskal–Wallis tests for differences in the mean densities of the three most abundant mollusc species (excluding *Littorina* spp.) at East Harbor, Truro, Massachusetts, by region and size class.

Species	*Size Class (cm)*	*Moon Pond (individuals/m^2) n = 10**	*Lagoon (individuals/m^2) n = 30**	*Cove (individuals/m^2) n = 10*	χ^2	*p*
Mercenaria mercenaria	Harvestable	0	0	0	–	–
	>4	0.66 ± 0.66	0	0	4.00	0.1353
	2–4	**4.66 ± 2.26**	**0.18 ± 0.15**	**0**	**14.36**	**0.0008**
	<2	12.73 ± 12.73	4.24 ± 2.95	0	0.98	0.6139
Mya arenaria	Harvestable*	24.84 ± 14.93	0.94 ± 0.29	0.22 ± 0.2	2.13	0.3448
	>4	**64.27 ± 31.46**	**3.56 ± 0.92**	**0.22 ± 0.22**	**8.94**	**0.0115**
	2–4	**77.48 ± 52.15**	**3.11 ± 1.50**	**0**	**9.85**	**0.0073**
	<2	**3,036.58 ± 1,800.35**	**2,964.43 ± 726.47**	**0**	**18.89**	**<0.0001**
Mytilus edulis	**>4**	**4.11 ± 2.96**	**0.04 ± 0.04**	**0**	**12.78**	**0.0017**
	2–4	**30.41 ± 22.39**	**0**	**0**	**17.00**	**0.0002**
	<2	**12.73 ± 8.49**	**0**	**0**	**8.17**	**0.0169**

Bold type indicates statistical significance at $p \leq 0.05$. Dashes indicate size classes for which no individuals were detected, and for which statistical analyses could not therefore be performed.
* The sample sizes for harvestable *Mya arenaria* in Moon Pond and the lagoon are $n = 8$ and $n = 26$, respectively.

Table 4. Species contributions (%) toward mean dissimilarity of species assemblages among regions at East Harbor, Truro, Massachusetts.

Species	*MP vs. L (76.2)*	*MP vs. C (98.7)*	*C vs. L (98.5)*
Mya arenaria	38.3	45.0	93.0
Gemma gemma	10.8	18.0	*
Mytilus edulis	6.2	13.4	*
Littorina spp.	5.5	10.9	1.0
Mercenaria mercenaria	3.9	4.0	2.4
Macoma balthica	*	3.5	*
Petricola pholadiformis	1.2	2.8	*
Mulinia lateralis	1.0	*	1.5
Geukensia demissa	*	*	1.5
Ensis directus	*	*	*
Order *Cephalaspidea*	*	*	*
Euspira heros	*	*	*
Spisula solidissima	*	*	*
Tagelus plebeius	*	*	*
Anomia spp.	*	*	*
Nucella lapillus	*	*	*

Data were square root transformed. Numbers in parentheses represent the mean dissimilarity (δ) between all pairs of intergroup samples for each pairwise comparison. Asterisks indicate negligible (<1%) contributions toward aggregate dissimilarity between regions. MP, Moon Pond; L, lagoon; C, northwest cove.

connecting East Harbor to Cape Cod Bay is a small fraction of the lagoon's total volume and therefore has no noticeable effect on the system's oxygen budget (Portnoy et al. 2005, 2006). Oxygen depletions at East Harbor in August 2006 were marked by massive *Mya arenaria* mortality (Portnoy et al. 2006); thus, continued summertime oxygen stress may also limit the full recovery of molluscan populations at East Harbor (Dauer 1993; Thiel et al. 1998; Gray et al. 2002). Increasing tidal flow to the system would likely improve water quality and further increase salinity levels throughout the lagoon and northwest cove (Portnoy 1991; Burdick et al. 1997; Konisky et al. 2006), with subsequent increases in molluscan diversity and abundance across all three regions.

Although some molluscs become sexually mature in as little as 1 year, others may take up to 5 years to reach maturity (Stanley & Dewitt 1983; Newell & Hidu 1986; Newell 1989). Because our sampling took place only 3 years after partial tidal flow was restored, many of the molluscs we detected likely originated in Cape Cod Bay and entered the East Harbor system as planktonic larvae. The high density of small (<2 cm) *Mya arenaria* throughout Moon Pond and the lagoon suggests, however, that this species may also be spawning within East Harbor. Direct comparison with data from nearby Barnstable Harbor (Hunt et al. 2003) is difficult, because site- and season-specific temperature, salinity, substrate, and hydrodynamic regimes all play a role in larval settlement and juvenile *Mya arenaria* growth (Brousseau 1978; Newell & Hidu 1986; Hunt et al. 2003). Nevertheless, mean abundance of juvenile *Mya arenaria* (2 mm–2 cm) at East Harbor was considerably higher than mean abundance of similar size classes in Barnstable (Hunt et al. 2003). Some of this difference may be attributed to the limited presence of predators at East Harbor in 2005 (B. Thelen 2005, Antioch University, New England, personal observation). As greater numbers of marine predators such as Green crab (*Carcinus maenas*) and Northern moonsnail (*Euspira heros*) migrate into East Harbor from Cape Cod Bay, abundance of juvenile *Mya arenaria* and other bivalves can thus be expected to decline (Hunt & Mullineaux 2002; Hunt et al. 2003). Preliminary data and observations of large quantities of drilled and chipped *Mya arenaria* shell from 2006 indicate that juvenile *Mya arenaria* populations at East Harbor have already begun to wane as a result of increased predation (D. Israel 2006, Cape Cod National Seashore, Wellfleet, MA, personal communication).

Two of the four most abundant species at East Harbor (*Mya arenaria* and *Me. mercenaria*) have been identified by Dauer (1993) as "equilibrium species," which are defined as relatively long-lived species that dominate community biomass in undisturbed habitats. Highly stressed macrobenthic communities are frequently dominated by shallow-dwelling, short-lived opportunistic species; therefore, the dominance of these two long-lived, equilibrium molluscan species at East Harbor indicates that the benthic habitat is physically stable and suitable for deep-dwelling macroinvertebrates. Given such suitable habitat, macroinvertebrate species richness and abundance at East Harbor may continue to increase as sea grass cover (Heck et al. 1995; Irlandi 1997; Smith 2005) and shell production (Dame et al. 2001; reviewed by Gutierrez et al. 2003) expand.

Long-term monitoring of benthic molluscan populations is now needed to fully assess the effectiveness of tidal restoration at East Harbor and to guide additional restoration efforts along the Atlantic and Gulf coasts. Future researchers should consider sampling the entire East Harbor lagoon using replicate grab samples (Hyland et al. 2004) to eliminate logistical difficulties associated with the shovel method at water depths greater than 0.3 m, and wet-sieving benthic core samples through finer scale (0.5 or 1.0 mm) mesh to detect molluscan postlarvae (Hartley 1982). Because sediment characteristics may significantly influence macrobenthic community structure (Gray 1974; Ricciardi & Bourget 1999; Hyland et al. 2004; Kennish et al. 2004; Poulton et al. 2004), future researchers should also analyze sediment composition at all sampling points. Last, measuring molluscan length and calculating molluscan biomass via the relationship between length and ash-free dry weight would allow for closer comparison with nekton communities at East Harbor and other estuarine restoration sites (Ricciardi & Bourget 1999; Neckles et al. 2002).

The abundance and widespread distribution of *Mya arenaria* at East Harbor, just 3 years after partial tidal flow restoration, demonstrate the resilience of molluscan communities in recovering estuaries, whereas the limited presence of molluscs in the northwest cove and northern edges of the lagoon illustrates the continued need for full tidal flushing. With more complete tidal restoration, East Harbor and other recovering estuaries along the Atlantic and Gulf coasts could potentially support recreational or commercial shellfisheries, which in turn could generate greater localized support for estuarine restoration initiatives in coastal communities throughout Europe and North America.

Implications for Practice

- Given suitable substrate, salinity, and proximity to source populations of benthic molluscs, benthic molluscan communities can begin to recover within 3 years of restoring tidal flow to tide-restricted estuaries; thus, even partial tidal restoration should be considered for estuarine systems still subject to full tidal restriction.
- If tidal flow is only partially restored, low salinity levels and summertime oxygen stress may limit the full recovery of molluscan populations at estuarine restoration sites. Managers should thus prioritize full tidal restoration whenever possible.
- Long-term monitoring of benthic macroinvertebrates, submerged aquatic vegetation, and marine predators is needed to fully gauge the effectiveness of tidal restoration efforts at East Harbor and other estuarine restoration sites.

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